

The exploitation of food resources by soil meso- and macro invertebrates

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Summary. A food web is presented for soil meso- and macroinvertebrates in grassland. It is based on field observations made using a large custom – built rhizotron which allows the soil ecosystem to be studied under natural conditions without disturbing the animals or their environment. The food web has many characteristics (e.g. number of trophic links, frequency distribution of food chain lengths, linkage density, connectance) in common with webs of similar size from other habitats but there are also important differences. There are unusually low proportions of trophic links between top and intermediate species and between intermediate species. The proportion of links with basal species is very high. We observed very few taxa specialized for catching and consuming live meso- or macroinvertebrates and those present were never abundant. Even top predators such as geophilomorph centipedes also exploited inanimate basal resources. Interactions between animal taxa may therefore be relatively rare and weak. There was a high degree of omnivory, no clear compartmentation, and separate herbivore and decomposer food webs could not be distinguished. Plant root systems were an important resource for many soil animals. There was evidence that certain taxa fed preferentially on different parts of the root system but there was no clear evidence for exclusive guilds or species packing.

Key words: Rhizotron, soil invertebrates, food web, feeding behaviour

Introduction

Due to the difficulty of observing soil animals under field conditions, their interactions with each other and with the various inanimate food resources available to them remains largely unknown or conjectural. As a result there have been few attempts at constructing food webs for soil animals. Those which have been published are not quantitative and rely on soil extractions to determine faunal composition after which assumptions are made about the animal's feeding behaviour which has often been determined in the laboratory rather than in the field (Hunt et al. 1987; Walter et al. 1988; Whitford 1989; Moore et al. 1990). This approach also takes no account of the relative importance of the various animal interactions and in some cases important food resources such as the plant root system have been ignored. Our paper represents the first attempt to build a comprehensive food web for soil meso- and macroinvertebrates based on field observations which is supported by

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quantitative data on feeding behaviour. We have overcome the problem of observation by using a large purpose – built rhizotron (Sackville Hamilton et al. 1991). This has enabled us to watch the behaviour of soil animals under natural field conditions over prolonged periods without disturbing them or their environment.

Materials and Methods

The rhizotron

The rhizotron is situated at Treborth, Bangor, in an amenity grassland which has been under grass for over forty years. The soil is a heavy clay loam. The building of the rhizotron has been described in detail by Sackville Hamilton et al. (1991). It contains 34 windows (90 cm × 50 cm) which allow the soil profile to be observed to a depth of 70 cm. Inside the rhizotron the windows are equipped with shutters to eliminate light and are backed by foam insulation to buffer them against temperature fluctuations. Each window looks out onto a separate 1 m² plot of land which is sown with mixed clover (*Trifolium repens* L. cv Grasslands Huia) and Italian rye-grass (*Lolium perenne* L. cv S24). During dry weather the plots around the rhizotron are irrigated to prevent the soil shrinking away from the windows.

Comparison of soil fauna observed from the rhizotron with that obtained by conventional soil extraction

This comparison was performed on 8 July 1991. Surveys were conducted (procedure described below) looking through the windows out on to 15 north-facing plots. After this an intact soil core (3.8 cm diameter × 10 cm depth) with turf was taken from the centre of each plot. The soil cores were extracted in a Burkhardt funnel extractor with light and heat source for ten days.

The food resources

Seven food resources were recognised: *Algae*.

Root system: This resource was further subdivided into root hairs, root tips, the main and lateral roots, transparent rootlets (<0.25 mm diameter) and clover root nodules. Apart from identifying feeding on clover nodules we did not distinguish between clover and rye-grass root systems. *Fungal hyphae and mycorrhizae*: Hyphae on living plant roots were classed as mycorrhizae, hyphae growing elsewhere were classed as fungal hyphae. Both were often small in size and difficult to identify with any certainty so it is possible that feeding on them has been underestimated. *Dead vegetation*: This resource was further subdivided into dead and decaying roots and the grass and clover leaves brought below ground by earthworms. *Carrion*: Only those bodies located below the soil surface were considered. *Faeces, detritus and the soil surfaces* (including the lining of earthworm burrows): It was not always possible to distinguish accurately which of these three an animal was feeding on so they have been grouped together as a single resource. Where it was possible to distinguish between them, it has been referred to in the text. The animals exploiting this complex of resources probably obtain much of their nutrition from 'microbe stripping' (Macfadyen 1979; Anderson & Cargill 1987) but it was beyond the scope of our study to determine trophic relationships at this level. Similarly, some of the animals may have been grazing on microscopic fungal hyphae but failure to distinguish this is an unavoidable limitation of this method of non-intrusive observation. *Live animals*: Due to limitations on the size of animal we could observe (see below), predation on microinvertebrates (e.g. nematodes, protozoa etc.) was not assessed.

The taxon groupings

The taxa recognised are listed in Table 1. As only ×10 magnification was used for observations we were unable to assess feeding by or on microinvertebrates. Some of the taxa are only included in the food web analysis as they were not observed to feed during the quantitative study period. Every effort was made to ensure that the taxon groupings were as specific as possible, although several (e.g. Acari) remain very broad. Identification was difficult, because to avoid disturbing the ecosystem we could not remove individual animals for detailed study and were restricted to observations through the glass

windows. Certain animals are so distinctive that they could readily be identified to species (e.g. *Boettgerilla pallens*). In other cases, subsequent work has shown that no similar closely related species are present (e.g. *Campodea lankestri*).

Analysis of data

The food web was derived from all the interactions observed between May 1989 and August 1991. The quantitative data on the importance of the various resources were obtained from 35 detailed surveys carried out between May and August 1989 and between August and October 1990 inclusive. Surveys were conducted in the mornings, and each window was observed for 10–15 minutes using a $\times 10$ handlens. All fauna present and their feeding activity were recorded. Illumination was provided by a studio photographic light set well back so as to minimise disturbance to photosensitive animals. The food web is based solely on field observations of undisturbed soil in an attempt to avoid the biases involved in laboratory feeding trials, and gut content analyses. Many soil invertebrates feed on animal or plant fluids or exploit the microflora and microfauna present in their food, which could not be observed.

Food web characteristics have been determined following the definitions given by Pimm et al. (1991). Top species feed on, but are not fed on by, other species in the web; basal species feed on nothing in the web, and intermediate species have both predators and prey within the web. Linkages are trophic connections between species. The food chain frequency distribution was calculated according to the procedure of Cohen et al. (1989). Linkage density was calculated as the total number of observed linkages divided by the total number of taxa. Connectance (the actual number of linkages as a proportion of the potential number of linkages) was calculated as: $C = \frac{2 \times S}{S^2}$ (C = Connectance,

S = Total number of trophic species). This formula was used rather than the more usual 'twice the number of observed linkages divided by $S(S - 1)$ ' because the web includes cannibalistic interactions (Pimm et al. 1991). As linkage density and connectance can be influenced by the way in which the data are organised, we calculated values in two ways:

(a) with the basal species as separately defined as possible (algae, root tips, root hairs, transparent rootlets, the main and lateral roots, clover nodules, fungal hyphae, mycorrhizae, decaying grass, decaying roots, carrion, faeces/detritus/soil surfaces). Although it could be argued that the various parts of the root system are essentially a single taxon we consider it not unreasonable to separate them, as their exploitation probably requires distinct morphological and physiological adaptations similar to those required by invertebrates exploiting the various above-ground parts of plants.

(b) with the basal species grouped together (algae, root, system, fungal hyphae mycorrhizae, decaying vegetation, carrion, faeces/detritus/soil surface). The extent to which omnivory occurs in food webs is subject to considerable debate which is hampered by its many different definitions (Pimm et al. 1991). We have calculated the degree of omnivory as the number of closed omnivorous links divided by the number of top predators (Sprules & Bowerman 1988). A closed omnivorous link exists when a feeding path can be traced to a prey more than one trophic level away and from that prey back to the predator through at least one other prey occupying an intermediate trophic level.

Results

The data for the food web are given in Table 1 and the web is illustrated in Figs. 1a and 1b. The web is very complex with the majority of animal taxa exploiting several basal resources. Food web characteristics are summarised in Table 2. Compared with the majority of food webs, ours contains an unusually high proportion of top predators. This may be due, at least partially, to the web being based solely on our own observational data. As the act of predation on animals is swift, it is seldom witnessed and this can result in many taxa apparently lacking predators and therefore being classed as top predators, even though they consume only basal species (but also see Discussion). This would also explain the relatively high predator:prey ratios. In the majority of food webs, the numbers of predators and prey are roughly proportional (Briand & Cohen 1984). It should be remembered that our soil system takes no account of species which eventually enter the above-ground system, such as earthworms or beetle and Diptera adults which are subsequently eaten by birds

Table 1. Food resources exploited by the soil meso- and macroinvertebrate fauna

[illegible]

			Main/ lateral/ roots	Clover nodules	Fungal hyphae	Mycor- rhizae	Decaying grass	Decaying roots	Carrion	Faeces/ detritus/ soil surfaces
20	Carabid/staphylinid larvae	(g)				×	×			
21	Curculionid adults									
22	Elatерid larvae		×							
	Diptera									
23	<i>Berris vallata</i> (Forster) larvae									
24	<i>Rhagio scolopacea</i> (L.) larvae		×	×						
25	Tipulid larvae									
26	Dipterous larvae	(h)								
	Hymenoptera									
27	<i>Lasius niger</i>		×		×	×				
28	Aphidoidea									
1	Earthworms	(a)	×	×		×	×	×	×	×
2	Enchytraeidae		×					×	×	×
	Planaria									
3	<i>Microplana scharffii</i> (von Graff)									
4	<i>Microplana terrestris</i> (Pantin)								×	
	Mollusca									
5	<i>Boettgerilla pallens</i> (Simroth)		×			×	×	×	×	×
6	Other slugs	(b)					×	×	×	
7	Isopoda	(c)			×	×		×		×
	Araneae									
8	Linyphiidae									
9	Acari	(d)	×						×	
	Diplopoda									
10	Iulidae	(e)	×						×	×
11	Polydesmidae		×					×		×
12	Diplopoda	(f)	×				×			
	Chilopoda									
13	Geophilomorpha								×	×
14	Lithobiomorpha									
15	Symphyla		×							×

Table 1. (Continued)

Trophic species number	Taxon	Trophic species consumed							
		Basal species							
		Main/lateral roots	Clover nodules	Fungal hyphae	Mycorrhizae	Decaying grass	Decaying roots	Carrion	Faeces/detritus/soil surfaces
	Insecta								
	Diplura								
16	<i>Campodea lankestri</i> (Silvestri)	×	×	×	×	×	×	×	×
17	Collembola	×	×	×	×	×	×	×	×
	Coleoptera								
18	Staphylinid adults							×	×
19	Carabid adults							×	
20	Carabid/staphylinid larvae	(g)						×	
21	Curculionid adults								×
22	Elaterid larvae	×				×			×
	Diptera								
23	<i>Berris vallata</i> (Forster) larvae	×						×	×
24	<i>Rhagio scolopacea</i> (L.) larvae								×
25	Tipulid larvae					×			
26	Dipterous larvae	(h) ×							
	Hymenoptera								×
27	<i>Lasius niger</i>								
28	Aphidoidea	×							

Notes: (a) these consisted of *Allolobophora chlorotica* (Savigny), *Apporrectodea caliginosa* (Savigny), *Ap. longa* (Ude), *Ap. rosea* (Savigny), *Lumbricus festivus* (Savigny), *L. castaneus* (Savigny), *L. terrestris* L., *L. rubellus* Hoffmeister, *Murchieona minuscula* (Rosa), *Octolasion cyaneum* (Savigny). (b) these consisted of: *Arion hortensis* (Férussac), *A. ater* (Linné), *Milax budapestensis* (Hazay), *Deroceras reticulatum* (Müller), *D. caruanae* (Pollonera). (c) these consisted of: *Trichoniscus pusillus* (Brandt) and *Haplophthalamus montivagus* (Verhoeff). (d) *Pergamasus quisquiliarius* (Mesostigmata) was the most frequently seen adult mite. Other mite species were not identified. (e) *Blaniulus guttulatus* (Fabricius) was the most abundant iulid but at least four other species were present. (f) where further identification was impossible. (g) it was not possible to distinguish the larvae of carabid and staphylinid beetles. (h) where further identification was impossible. (× indicates that at least one observation of feeding was recorded)

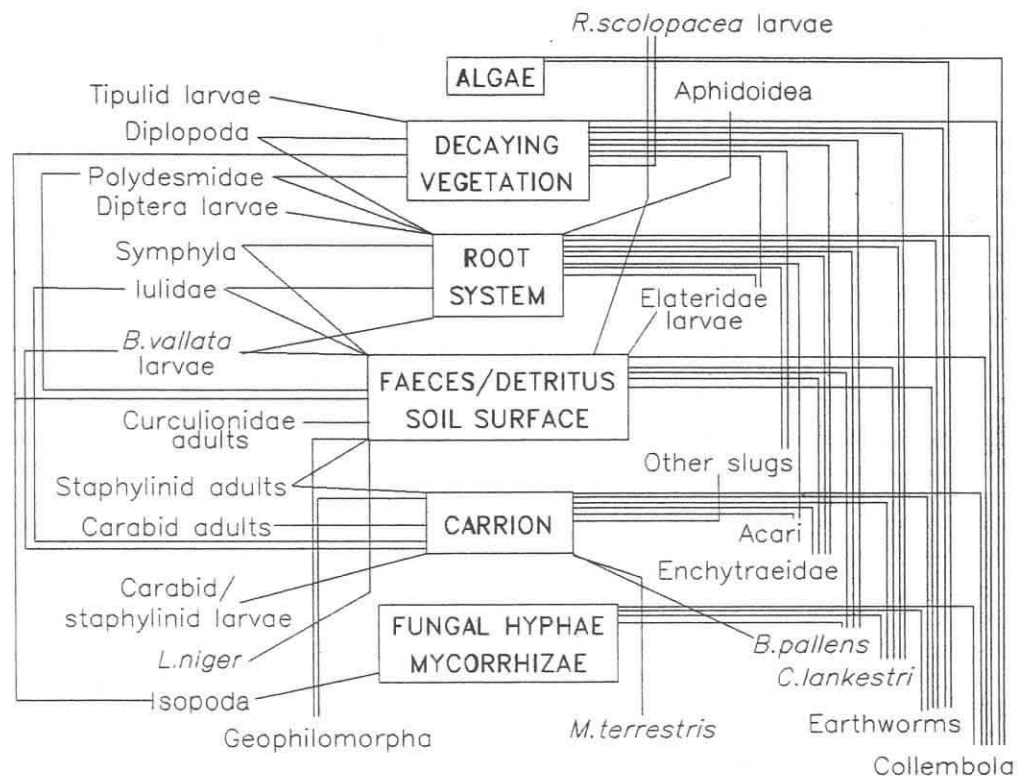


Fig. 1a. Food web based on the observed interactions of the soil meso- and macroinvertebrate fauna with their inanimate (basal species) resources. For descriptions of taxa see text and Table 1

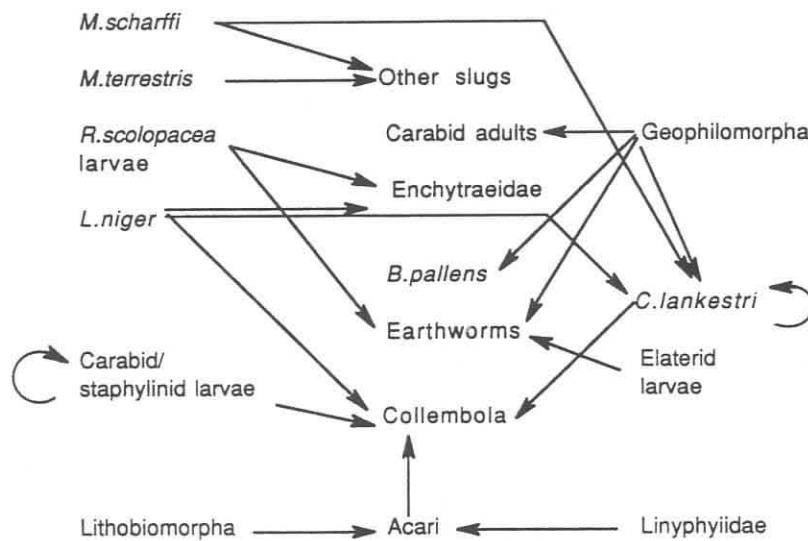


Fig. 1b. Food web based on the observed animal:animal interactions within the soil meso- and macroinvertebrates. For descriptions of taxa see text and Table 1

Table 2. Food web characteristics

Web characteristic	Basal groupings subdivided	Basal species grouped
Number of trophic species	40	34
Number of animal taxa	28	28
Proportion top series ()	0.53 (0.16)	0.60 (0.18)
Proportion intermediate species ()	0.20 (0.57)	0.24 (0.66)
Proportion basal species ()	0.27 (0.27)	0.16 (0.16)
Predator:prey ratio	1.33	1.87
Number of trophic links	105	82
Proportion links top – intermediate ()	0.14 (0.13)	0.18 (0.17)
Proportion links top – basal ()	0.30 (0.05)	0.36 (0.06)
Proportion links intermediate – intermediate ()	0.05 (0.05)	0.06 (0.06)
Proportion links intermediate – basal ()	0.30 (0.77)	0.40 (0.71)
Number of food chains	266	154
Length of food chains	1–4	1–4
Mean food chain length	2.504	2.344
Modal food chain length	2	2
Linkage density	2.625	2.412
Connectance	0.131	0.142
Number of closed omnivorous links	26	26
Degree of omnivory	1.22	4.00
Number of omnivores (trophic species)	8	9

() = restricted definition of top predator (see text)

and mammals and which would be regarded as basal or low intermediate trophic species in those systems. The soil system is not sharply delineated. If the number of top predators is restricted to *Microplana scharffi*, *M. terrestris*, Linyphiidae, Geophilomorpha, Lithobiomorpha, *Rhagio scolopacea* larvae, and *Lasius niger*, all of which feed primarily on other animals but are not themselves consumed, then the ratios of top predators, intermediate species and basal species become similar to those of other webs (see Briand & Cohen 1984). Grouping the basal species has little impact on the proportions.

Cohen et al. (1986) suggested that the number of trophic links (L) in a food web is related to the number of trophic species (S) according to the equation $L = 0.6713 S^{1.36}$. Our food web should therefore contain 101 (basal groupings subdivided) or 81 (basal species grouped) trophic links. These calculations are remarkably close to the number of links actually observed (105 and 82) and are in line with the trend observed by Brian & Cohen (1987) in their analysis of 113 published food webs. According to Cohen & Briand (1984) the proportions of trophic links between top and intermediate, top and basal, intermediate and intermediate, and intermediate and basal species are roughly constant between webs of various sizes and from different habitats. Our results however, fall well outside their quoted values regardless of the classification of the top predators used, and this reflects the importance of trophic links to basal species and a paucity of links between intermediate species, and intermediate species and top predators.

The frequency distribution of food chains is shown in Fig. 2. The modal food chain length was 2. These results are typical of food webs containing around 30 trophic species (Cohen et al. 1986). Grouping the basal species caused a slight increase in the proportion of single link chains and a reduction in the proportions of 3 and 4 link chains but the proportion of 2 link chains was not affected.

Connectance is a function of the number of vertical links in the food web and is considered to influence community stability (May 1973). Plots of connectance versus the number of trophic species assume a hyperbolic form and our values are typical (Cohen & Newman 1988; Paine 1988). To estimate the degree of omnivory the following trophic levels were adopted:

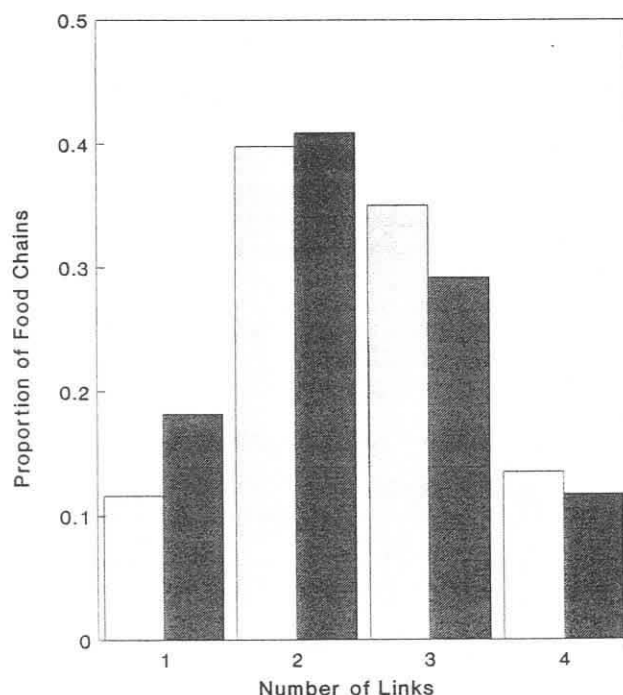


Fig. 2. Frequency distribution of food chain lengths

Level 1. Basal species.

Level 2. Intermediate species consuming only basal species: earthworms, Enchytraeidae, *B. pallens*, other slugs, Isopoda, Iulidae, Polydesmidae, Diplopoda, Symphyla, Collembola, staphylinid adults, carabid adults, curculionid adults, *Berris vallata* larvae, tipulid larvae, Diptera larvae, Aphidoidea.

Level 3. Intermediate species consuming both basal and intermediate species: Acari, *C. lankestri*, carabid/staphylinid larvae, elaterid larvae.

Level 4. Top predators: *M. scharffi*, *M. terrestris*, Linyphiidae, Geophilomorpha, Lithobiomorpha, *R. scolopacea* larvae, *L. niger*.

8 omnivores were recognized (*M. terrestris*, Geophilomorpha, Acari, *C. lankestri*, carabid/staphylinid larvae, elaterid larvae, *R. scolopacea* larvae, *L. niger*) which corresponds to 20% (basal groupings subdivided) or 23.53% (basal species grouped) of the trophic species and 28.57% of the animal taxa. There were 26 closed omnivorous links and the degree of omnivory (calculated using the restricted definition of top predators) was 4. The criticism that the degree of omnivory may be artificially enhanced, because of grouping taxa containing diverse species, does not apply here as 50% of the omnivores are specific taxa and, with the exception of the Acari, the others include species with very similar feeding habits.

Cycles occur in food webs where for example, (a) eats (a) (cannibalism), (a) eats (b) and (b) eats (a) or (a) eats (b), (b) eats (c) and (c) eats (a). Such cycles are considered rare in community food webs (Pimm et al. 1991) and only two cycles were observed in our web, both due to cannibalism by *C. lankestri* and carabid/staphylinid larvae. However, if necrophages are not selective over which corpses they consume, there are potentially 14 direct cycles (feeding on corpses of their own taxon) and at least 18 indirect cycles (e.g. top predator feeding on intermediate species feeding on the corpse of a top predator). Such cycles have been observed (e.g. Collembola → corpse of Collembola; *L. niger* → *C. lankestri* → corpse of *L. niger*).

Table 3. Composition of the soil meso- and macroinvertebrate fauna as determined by a rhizotron survey and by soil extractions from cores taken on the same day from adjacent land. (For details see text)

Taxon	Rhizotron survey						Soil Extraction					
	Total	%	Mean	Min	Max	S.E.	Total	%	Mean	Min	Max	S.E.
Total animals	412		27.67	10	71	4.660	397	1.3	26.50	0	108	6.970
Earthworms	46	11.2	3.07	0	10	0.628	5	3.0	0.33	0	2	0.159
Enchytraeidae	22	5.3	1.47	0	8	0.542	12		0.80	0	4	0.327
<i>Microplana scharffi</i>	1	0.2	0.07	0	1	0.067	NR					
<i>Boettgerilla pallens</i>	6	1.5	0.40	0	2	0.163	NR					
Other slugs	16	3.9	1.07	0	3	0.284	NR					
Snails	NR						1	0.2	0.07	0	1	0.067
Isopoda	1	0.2	0.07	0	1	0.067	NR					
Linyphiidae	NR						1	0.2	0.07	0	1	0.067
Acari	5	1.2	0.33	0	2	0.159	236	59.4	15.70	0	65	4.640
Tick	NR						1	0.2	0.07	0	1	0.067
Geophilomorpha	2	0.5	0.13	0	1	0.091	NR					
Symphyla	2	0.5	0.13	0	1	0.091	NR					
<i>Campodea lankestri</i>	16	3.9	1.07	0	7	0.511	NR					
Collembola	288	69.9	19.20	4	66	4.870	132	33.2	8.80	0	43	2.850
Staphylinid adults	1	0.2	0.07	0	1	0.067	NR					
Carabid/staphylinid larvae	2	0.5	0.13	0	2	0.133	3	0.8	0.20	0	2	0.145
Elateridae larvae	NR						1	0.2	0.07	0	1	0.067
Tipulid larvae	1	0.2	0.07	0	1	0.067	NR					
Nematocerca larvae	NR						4	1.0	0.27	0	4	0.267
<i>Lonchoptera lutea</i> larvae	2	0.5	0.13	1	1	0.091	NR					
Diptera larvae	1	0.2	0.07	0	1	0.067	NR					
Psocoptera	NR						1	0.2	0.07	0	1	0.067

The rhizotron survey and soil extractions yielded somewhat different pictures of the composition of the soil fauna (Table 3). The soil cores contained large numbers of Acari but very few were seen through the rhizotron windows. Conversely the rhizotron survey indicated a more diverse soil fauna with significant numbers of *B. pallens*, 'other slugs' and *C. lankestris* which were not found in the soil cores. The differences are unlikely to be due to analysing the soil to different depths as the majority of soil meso- and macroinvertebrates at Treborth are found in the top 10 cm (unpublished results).

Table 4 lists all the taxa seen during the quantitative survey period, the number of times individuals were seen, the percentage of these sightings where feeding was observed, and the total number of food resources they utilised. This clearly shows that the majority of the soil invertebrates exploit many different food resources (polyphagy). A criticism of all grouping into taxa is that some include large and diverse groups of species which may have markedly different food requirements. This is undoubtedly the case for some (e.g.

Table 4. The taxa observed during the quantitative survey period (May–August 1989 and August–October 1990 inclusive): the number of times they were seen, and the percentage seen feeding during this period. The number of trophic species exploited in all surveys refers to data in Table 1. For details of taxa see Table 1 and text. A = basal groupings subdivided, B = basal species grouped

Number of trophic species exploited in all surveys		Taxon	Number (percentage) of all organism sightings in the soil	Number (percentage) of all the individual sightings in the taxon where feeding was seen
A	B			
12	6	Collembola	2730 (28.93)	1924 (70.48)
10	6	Earthworms	2718 (28.81)	1104 (40.62)
11	7	<i>Campodea lankestri</i>	1046 (11.09)	139 (13.29)
5	4	Enchytraeidae	788 (8.35)	186 (23.60)
3	3	Acari	576 (6.10)	7 (1.22)
8	5	<i>Boettgerilla pallens</i>	478 (5.07)	11 (2.30)
4	3	Other slugs	297 (3.15)	4 (1.35)
3	3	Staphylinid/ carabid larvae	159 (1.68)	9 (5.66)
3	3	<i>Berris vallatta</i> larvae	134 (1.42)	24 (17.91)
1	1	Carabid adults	101 (1.07)	0 (0)
2	2	Staphylinid adults	98 (1.04)	5 (5.10)
6	6	Geophilomorpha	78 (0.83)	4 (5.13)
4	3	Isopoda	54 (0.57)	9 (16.67)
2	2	Symphyla	31 (0.33)	6 (19.35)
3	3	Iulidae	26 (0.28)	2 (7.69)
2	2	<i>Microplana scharffi</i>	23 (0.24)	1 (4.35)
0	0	<i>Lonchoptera lutea</i> larvae	22 (0.23)	0 (0)
3	3	<i>Rhagio scolopaceae</i> larvae	16 (0.17)	0 (0)
4	4	Elaterid larvae	11 (0.12)	6 (54.55)
1	1	Lithobiomorpha	11 (0.12)	0 (0)
2	2	Diplopoda	9 (0.09)	1 (11.11)
4	3	Polydesmidae	8 (0.08)	2 (25.00)
4	4	<i>Lasius niger</i>	6 (0.06)	0 (0)
1	1	Curculionid adults	6 (0.06)	1 (16.67)
2	2	<i>Microplana terrestris</i>	2 (0.02)	0 (0)
1	1	Dipterous larvae	2 (0.02)	1 (50.00)
1	1	Linyphiidae	2 (0.02)	1 (50.00)
1	1	Tipulid larvae	1 (0.01)	0 (0)
0	0	Dipterous adults	1 (0.01)	0 (0)

Acari), on the other hand both *C. lankestri* and *B. pallens* are specific taxa which are highly polyphagous. Moreover, in the case of *B. pallens* very few instances of feeding were seen. Table 5 illustrates the contribution of the various food resources as a percentage of each taxon's individual feeding activity, while Table 6 shows the contribution of the taxa as exploiters of each food resource.

Algae were exploited only by earthworms and Collembola and formed just a small percentage of their overall feeding. The main and lateral roots were the regions of the root system exploited by the largest number of taxa although *C. lankestri* and the Collembola together accounted for 74.36% of all the observed attacks on this region. Many animals e.g. earthworms, Enchytraeidae, *B. vallata* larvae, *C. lankestri*, Collembola and the majority of the Diplopoda confined their feeding activity to scraping or sucking at the root surface. This produced little or no observable damage. However, if the root was still young and white, then feeding by Symphyla, Collembola and *C. lankestri* was often prolonged and would result in the root being eaten through so killing the distal portion. Only three taxa fed on the minor transparent rootlets, earthworms being the most important. Earthworms consumed these rootlets either individually or, more commonly, while simultaneously ingesting soil-especially when feeding close to the soil surface where there was a well developed root mat. Root hairs were especially attractive to Collembola and other insects. Earthworms almost certainly ingested root hairs which would break off as they sucked at the surface of roots, but it was impossible to quantify. The root tip is probably a particularly important food resource for both *C. lankestri* and the Collembola, although both taxa also exploit the rest of the root system. The number of root tips that are accessible to the soil fauna at any one time is small as most do not occur in the cavities or tunnels where non-fossorial species can reach them. Consequently the numbers of these insects observed feeding on them are much higher than one would expect if feeding was indiscriminate. Individual *C. lankestri* and Collembola would sometimes spend over 60 mins. feeding on a single root tip and this would result in it becoming completely eaten away. Surprisingly, in view of their high nitrogen content, clover root nodules were very rarely attacked, suggesting some deterrents to feeding.

Fungal hyphae and mycorrhizae were exploited by only five taxa and formed only a small percentage of their overall feeding activity although this is probably an underestimate (see Materials and methods).

Although decaying vegetable matter was almost always readily accessible to all the soil fauna in one form or another, and many taxa exploited it as a food resource, it seldom formed a large percentage of their overall feeding.

Carriion was the least abundant food resource but figured prominently in the diets of many of the taxa. Those taxa which did feed on carriion did so intensively, rather than simply taking a few bites then moving elsewhere. Collembola (and in particular the Onychiuridae) were especially attracted to dead animals and would begin to feed on them before they had started to decay.

Faeces, detritus and soil surfaces are ubiquitous in the soil ecosystem and form the most readily accessible of all the food resources, so it is not surprising that so many taxa exploit them and that they form a relatively large (> 20%) fraction of overall feeding. Earthworms, Enchytraeidae, *B. pallens*, Isopoda, Collembola and iulid millipedes would frequently feed intensively on soil surfaces and/or earthworm faeces, while the Symphyla and the rest of the Insecta seldom fed on them intensively but tended to 'pick' briefly before moving elsewhere.

The geophilomorph centipedes showed no preference for particular prey species and due to their size and abundance throughout the year, are probably the most important predators in this soil system. Specimens of the ant *L. niger* preyed on any small invertebrate which blundered into the network of horizontal channels they constructed just below the soil surface. They did not forage at lower soil depths, and it is unlikely that they are as important predators in the soil system as they are above ground. In addition to preying on other animals the ants also tended small colonies of root-feeding aphids, and frequently collected honeydew from them.

Table 5. The contribution of various food resources as a percentage of each taxon's individual feeding activity during the quantitative survey period (May–August 1989 and August–October 1990 inclusive). (For details of taxa see Table 1 and text)

Food Resource														
Taxon	Algae	Root tips	Rot hairs	Trans-parent rootlets	Main/lateral roots	Clover nodules	Fungal hyphae	Mycor-rhizae	Decay-ing grass	Decay-ing roots	Car-rion	Faeces/detritus/soil surfaces	Live ani-mals	(Animals attacked)
Earthworms	3.83			7.21	0.68			0.22	16.67	1.13	2.03	68.24		
Enychtraeidae			2.08		1.39					15.62	2.78	78.14		
<i>Microplana scharffi</i>													100	<i>C. lankestri</i>
<i>Boettgerilla pallens</i>		16.7	8.33		8.33			16.67	16.67	16.67		16.67		
Other slugs		25.00							50.00	25.00				
Isopoda							8.33	8.33		16.67		66.67		
Linyphiidae													100	Acari
Acari					42.86						42.86		14.28	Collembola
Iulidae					50.00							50.00		
Polydesmidae					50.00					50.00				
Diplopoda					100									
Geophilomorpha													100	Earthworms (25%) <i>B. pallens</i> (25%) <i>C. lankestri</i> (25%) Carabid adult (25%)
Symphyla					33.35							66.65		
<i>Campodea lankestri</i>		7.89	1.43	5.02	14.34					2.15	15.78	51.94	1.43	<i>C. lankestri</i> (50%) Collembola (50%)
Collembola	0.11	0.44	2.74	0.27	2.08	0.06	0.60	0.77	0.16	0.38	12.41	79.97		
Staphylinid adults											80.01	19.99		
Curculionid adults												100		
Carabid/staphylinid larvae											66.66		33.34	Collembola (67%) Carabid/staphylinid larvae (33%)
Elaterid larvae					33.33				16.67			50.00		
<i>Berris vallata</i> larvae					25.00						50.00	25.00		
Dipterous larvae					100									

Table 6. The contribution of the different taxa as consumers of the various food resources. This is expressed as the number of times the resource was fed on by each taxon during the quantitative survey period (May–August 1989 and August–October 1990 inclusive) as a percentage of all instances of feeding observed (N). (For details of taxa see Table 1 and text)

Resource	N	Trophic species	Importance (%)	Resource	N	Trophic species	Importance (%)
Algae	19	Earthworms	89.47	Decaying grass	82	<i>Boettgerilla pallens</i>	2.44
		Collembola	10.53			Other slugs	2.44
Root tip	24	<i>Campodea lankestri</i>	45.83			Elaterid larvae	1.22
		Collembola	41.67	Decaying roots	25	Collembola	28.00
		<i>Boettgerilla pallens</i>	8.33			Earthworms	20.00
		Other slugs	4.17			Enchytraeidae	16.00
Root hairs	59	Collembola	84.74			<i>Campodea lankestri</i>	12.00
		Enchytraeidae	10.17			Isopoda	8.00
		<i>Campodea lankestri</i>	3.34			<i>Boettgerilla pallens</i>	8.00
		<i>Boettgerilla pallens</i>	1.69			Other slugs	4.00
Transparent rootlets	42	Earthworms	76.19			Polydesmidae	4.00
		<i>Campodea lankestri</i>	16.67	Carion	293	Collembola	81.57
		Collembola	7.14			<i>Campodea lankestri</i>	7.51
Main/lateral roots	78	Collembola	48.72			Earthworms	3.07
		<i>Campodea lankestri</i>	25.64			Enchytraeidae	2.73
		Enchytraeidae	5.13			Carabid/staphylinid larvae	2.05
		Earthworms	3.85			Staphilinid adults	1.37
		Acari	3.85			Acari	1.02
		Symphyla	2.56			<i>Berris vallata</i> larvae	0.68
		Elaterid larvae	2.56	Faeces/detritus/ soil surfaces	945	Collembola	62.96
		Iulidae	1.28			Earthworms	32.06
		Polydesmidae	1.28			<i>Campodea lankestri</i>	1.90
		Diplopoda	1.28			Enchytraeidae	1.06
		<i>Boettgerilla pallens</i>	1.28			Isopoda	0.63
		<i>Berris vallata</i> larvae	1.28			Symphyla	0.42
		Diptera larvae	1.28			Elaterid larvae	0.32
Clover nodules	2	Collembola	100.00			<i>Boettgerilla pallens</i>	0.21
Fungal hyphae	12	Collembola	91.67			Iulidae	0.11
		Isopoda	8.33			Staphylinid adults	0.11
Mycorrhizae	18	Collembola	77.78			Curculionid adults	0.11
		<i>Boettgerilla pallens</i>	11.11			<i>Berris vallata</i> larvae	0.11
		Isopoda	5.55	Live animals	12	Geophilomorpha	33.33
		Earthworms	5.55			Carabid/staphylinid larvae	25.00
Decaying grass	82	Earthworms	90.24			<i>Campodea lankestri</i> larvae	16.67
		Collembola	3.66			Acari	8.33
						Linyphiidae	8.33
						<i>Microplana scharffi</i>	8.33

Discussion

Although our food web has many characteristics (e.g. number of trophic links, frequency distribution of food chain lengths, linkage density, connectance) in common with webs of similar size from other habitats it also has certain important differences. The low proportions of trophic links between top and intermediate species and intermediate and intermediate species may be partially due to the way the data were collected but probably also reflects the nature of the soil system. We observed very few taxa specialized for catching and consuming live meso- or macroinvertebrates and those present were never abundant. Even top predators such as geophilomorph centipedes also exploited inanimate basal resources. Interactions between animal taxa may therefore be relatively rare and weak. The importance of predators in the soil system is still undecided. Swift et al. (1979) suggested that predators are important in regulating the detritivore population and hence the rate and pattern of decomposition while Andersen (1987) considered the role of predators in determining the distribution and abundance of soil herbivores to be still unclear. As many soil animals feed on both plant roots and dead organic matter, and the growth of plant roots is influenced directly by herbivory and indirectly by the release of nutrients from dead organic matter, the possible effects a predator may have on the system as a whole can be expected to be extremely complex.

Omnivory was more prevalent than in the majority of food webs although similar levels have been recorded in aquatic ecosystems which are decomposer-based (Warren 1989; Hall & Raffaelli 1991). A similar lack of specialization coupled with a marked diversity of feeding behaviour among even closely related species has been demonstrated among predatory arthropods inhabiting shortgrass steppe soil (Walter et al. 1988). Apart from the possibility that omnivory may have been underestimated in many food webs due to the way in which the data were collected (Lawton 1989; Hall & Raffaelli 1991), it is also thought to be characteristic of animals living in constant environments (Lawton 1989). The soil environment is more constant than that above ground although growth of roots and the supply of dead organic matter is highly seasonal. Heavy rain can also alter soil characteristics rapidly (e.g. oxygen availability and living space). Swift et al. (1979) recognized that members of the soil fauna may act at several trophic levels but claimed that the members of the herbivore subsystem (within which they include the predators of herbivores), could be 'readily ascribed a trophic position within clearly defined food chains' and that 'predators do not generally have any direct involvement in the decomposition process'. In our soil system herbivore and decomposer food webs could not be so easily separated. There was no clear compartmentation and the quantitative feeding behaviour studies indicate that the majority of soil meso- and macroinvertebrates commonly exploit a wide range of food resources. Given the widespread necrophagy many of the taxa could even be said to be joined in death. By contrast Moore & Hunt (1988) and Moore et al. (1990), using statistical analysis, were able to compartment soil food webs into categories of functional groups based on food choice and trophic level. There is still some debate over whether a high proportion of omnivores destabilises web dynamics (Pimm & Lawton 1977, 1978; Lawton 1989) although in model donor-controlled systems, which are closest to those of decomposer-based webs (Hall & Raffaelli 1991), they have no deleterious effect (Cohen et al. 1989). Ingham et al. (1986) have suggested that the ability of predators to use more than one prey group may actually have a stabilising influence.

The composition of our soil fauna differs in several respects from that recorded by other authors for temperate grass-land. In the majority of soil systems (which have usually been surveyed using soil extraction methods) the Acari are the most abundant of the soil fauna (Wallwork 1970). We found large numbers of mites in soil cores but observed very few during rhizotron surveys. This suggests the majority of mites at Treborth either live on the soil surface, and therefore would not be observed with the rhizotron, or significant numbers of the smallest species are remaining uncounted. Diplura are seldom observed in soil animal surveys using conventional extraction methods (e.g. Lagerlof & Andren 1991) although

our rhizotron surveys suggest *Campodea lankestri* is among the most abundant soil animals throughout the year (Gunn 1992a). Diplura are highly active insects and many probably escape during sampling. As they are so fragile some may be killed by soil compaction caused by coring and so would not be detected by behavioural extraction techniques. *Boettgerilla pallens* is a recent introduction to the British Isles (Colville 1974), and already has a widespread distribution (North & Bailey 1989). Unlike other slugs it spends virtually all its life below ground, and this coupled with its abundance and large size suggest that it has a significant role within the soil ecosystem (Gunn 1992b). We believe rhizotron surveys provide a good indication of the composition of the soil fauna albeit one rather different from that revealed by soil extraction methods. As the soil was kept moist, cracks leading from the soil surface did not develop. We were therefore examining undisturbed soil profiles rather than artificially deep cracks.

Only recently has the importance of below-ground herbivory been recognised (see reviews by Andersen 1987; Stanton 1988; Brown & Gange 1990). This study demonstrates that plant root systems are an important food resource for many soil animals. There was evidence that certain taxa fed preferentially on different parts of the root system (e.g. *C. lankestri* and Collembola fed on root tips, earthworms on transparent rootlets) but there was no clear evidence for the exclusive guilds or species packing which are common phenomena among above-ground herbivores. This is interesting as species packing and the resultant species diversity are often thought to arise as a consequence of competition for limited resources (Schoener 1974; Roughgarden 1983) and the soil environment is considered to be resource-poor for animals. Guilds of insect herbivores exploiting specific niches on the root system of the knapweeds *Centaurea diffusa* (Lam.), *C. maculosa* (Lam.) and *C. vallesiaca* (Jordan) have however, been described by Müller (1989) and Müller et al. (1989).

It was interesting to find that earthworms were the most important consumers of transparent rootlets. The gut contents of earthworms have frequently been shown to include root fragments (e.g. Bouché & Kretzschmar 1974; Pearce 1978) but these were thought to result from the worms feeding on dead and decaying roots. However, Baylis et al. (1986) found that the earthworms *Lumbricus rubellus*, *Aporrectodea caliginosa* and *Ap. longa* extracted from the soil surrounding clover plants labelled with ^{32}P had themselves become strongly radiolabelled as had small numbers of Enchytraeidae. They suggested that these animals were feeding on living roots, and this is confirmed in our observations.

Plant roots are frequently considered to be nutritionally inferior (especially in nitrogen) to foliage (Chapin et al. 1980; Seastedt 1985) although roots acting as storage organs may be nutritionally superior during winter. Despite this, several of the taxa (e.g. Collembola, *C. lankestri*, Diplopoda, Enchytraeidae) which might be expected to exploit the considerable quantities of grass leaves brought below ground by the earthworms either ignored them or fed very sparingly regardless of their state of freshness or decay.

Dead animal matter does not present the same physical barriers to its consumption as dead plant matter and is more rewarding nutritionally. It is not surprising therefore that it is so important in the diet of so many soil animals. However, carrion is relatively scarce and none of the soil fauna fed exclusively on it. To some extent, the animals observed feeding on a corpse depended on its size, smaller bodies (< 10 mm) being consumed mainly by the smaller insects and in particular the Collembola and *C. lankestri*. The death of large animals, such as mature slugs, would often precipitate a 'free for all' involving the majority of the soil fauna, including the small species. This modifies the cascade theory of food web structure (Cohen et al. 1989) so appropriate to predators, by having only a lower boundary to the size of food it is worth exploiting.

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